FOOD AVAILABILITY, REPRODUCTION, AND CONDITION OF EUROPEAN WILD BOAR IN GREAT SMOKY MOUNTAINS NATIONAL PARK

RESEARCH/RESOURCES MANAGEMENT REPORT No. 43

U.S. DEPARTMENT OF THE INTERIOR
NATIONAL PARK SERVICE
SOUTHEAST REGION

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January 1981

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Singer, Francis J. and Bruce B. Ackerman. 1981. Food Availability, Reproduction, and Condition of European Wild Boar in Great Smoky Mountains National Park. U.S. Department of the Interior, National Park Service, NPS-SER Research/Resources Management Report No. 43. 52 pp.

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ABSTRACT

A total of 550 European wild boar (_Sus scrofa L._) were collected during 42 months, 1976-80, from an exotic population invading Great Smoky Mountains National Park. Population size was low in 1976 following a mast failure, then increased an estimated 46% and declined 4% following two successive good mast crops in 1977 and 1978, respectively, and then declined 64% following a mast failure in 1979. Corresponding mast production on a 34.1 km^2 winter range study area averaged 17.7 $\pm$ 2.3, 60.6 $\pm$ 7.7, and 3.3 $\pm$ 0.4 kg/ha during successive Septembers. Seven blood chemistry and hematological parameters were not different between collections made during the winter following mast failures and the high elevations in summer but they were significantly greater from collections during summers at low elevations and in winter following an abundant mast crop for albumin, cholesterol, uric acid, calcium, electrolyte balance, packed cell volume, and white blood cells ($P < 0.05$). During February-March of 1979, 6-7 months following the mast failure, 11 wild boar were found dead or dying of malnutrition. From September-August of each year, 60 litters were produced per 100 breeding-aged females in 1975-76 following moderate acorn production, 73 litters per 100 females in 1976-77 and 59 litters per 100 females in 1977-78 following abundant mast crops; only 13 litters per 100 females were produced in 1978-79 following a mast failure.

INTRODUCTION

European wild boar were introduced to the southern Appalachian ecosystem about 1912 (Stegeman, 1938) and entered Great Smoky Mountains National Park (GRSM) sometime between 1948 and the early 1950's (Bratton, 1975; Fox and Pelton, 1978). The population inbred with resident feral swine (Sus scrofa) during the invasion (Rary et al., 1968) but still exhibit most characteristics typical of wild boar -- longitudinally striped piglets, split grey-brown hair tips, uniform agouti pelage, seasonal migrations, and fewer teats -- and are referred to as European wild boar for convention (Bratton, 1977). Feral pigs have occupied coastal southeastern United States for periods of 160 to 400 years, and their populations are now relatively stable (Wood and Lynn, 1977); however, wild boar are of relatively recent origin. They are invading new habitat at an average rate of 2.75 km per year, and much potential range remains for them in the Appalachian Mountains (Singer, in press). In their new range, wild boar are viewed as both a prized game species (Decker, 1978) and as a pest exotic with great potential for disturbing native ecosystems (Bratton, 1975; Wood and Barrett, 1979). The National Park Service leads the list of agencies with concerns over non-native pig populations (Wood and Barrett, 1979). Their mission is to protect native species, natural ecosystems and natural processes. GRSM is a large, roadless area where public hunting is not allowed and large predators are now extirpated, thereby reducing abilities to control wild pigs.

STUDY AREA

We collected 550 European wild boar from the well-occupied western one-half of GRSM. Scattered populations exist in the eastern half, and incursions into the unoccupied southeastern quarter by a few individuals occurred both in 1975 (Bratton, pers. comm.) and in 1978-79 during mast failures (Singer et al., in press) (Fig. 1).

Altitudinal migrations of wild boar in GRSM were rather abruptly upward in April to the northern hardwood zone and downward in August to low elevation oak/pine habitat (Singer et al., in press). Every year when it was available, hard mast (Quercus spp., Carya spp.) comprised 60% - 85% by volume of the wild boar diet (Henry and Conley, 1972; Scott and Pelton, 1975). When the mast crop fails, alternate foods, particularly wild yam tubers (Dioscorea batatas) and other roots, comprised 83% - 91% of the diets, and hard mast dropped to less than 10% (Henry and Conley, 1972; Scott and Pelton, 1975; Bratton et al., in press). In the northern hardwoods at high elevations in summer, corms and tubers comprised 40% of the diet and green herbaceous vegetation, 55% (Howe et al., in press). A few animals remain at low elevations in the summer. Their diets averaged 46.5% green leaves and stems and 5.7% roots and tubers (Scott and Pelton, 1975).

The National Park Service has attempted to control European wild boar along the limited road system since 1959; however, the Park's activities were greatly influenced by accessibility. Management activities were greatly accelerated in September 1976 and for the first time, animals were collected in the remote backcountry.

The low elevation winter range selected for study (34.1 km^2) was 49% yellow pine-oak (Pinus virginiana, Quercus spp.) forest type,

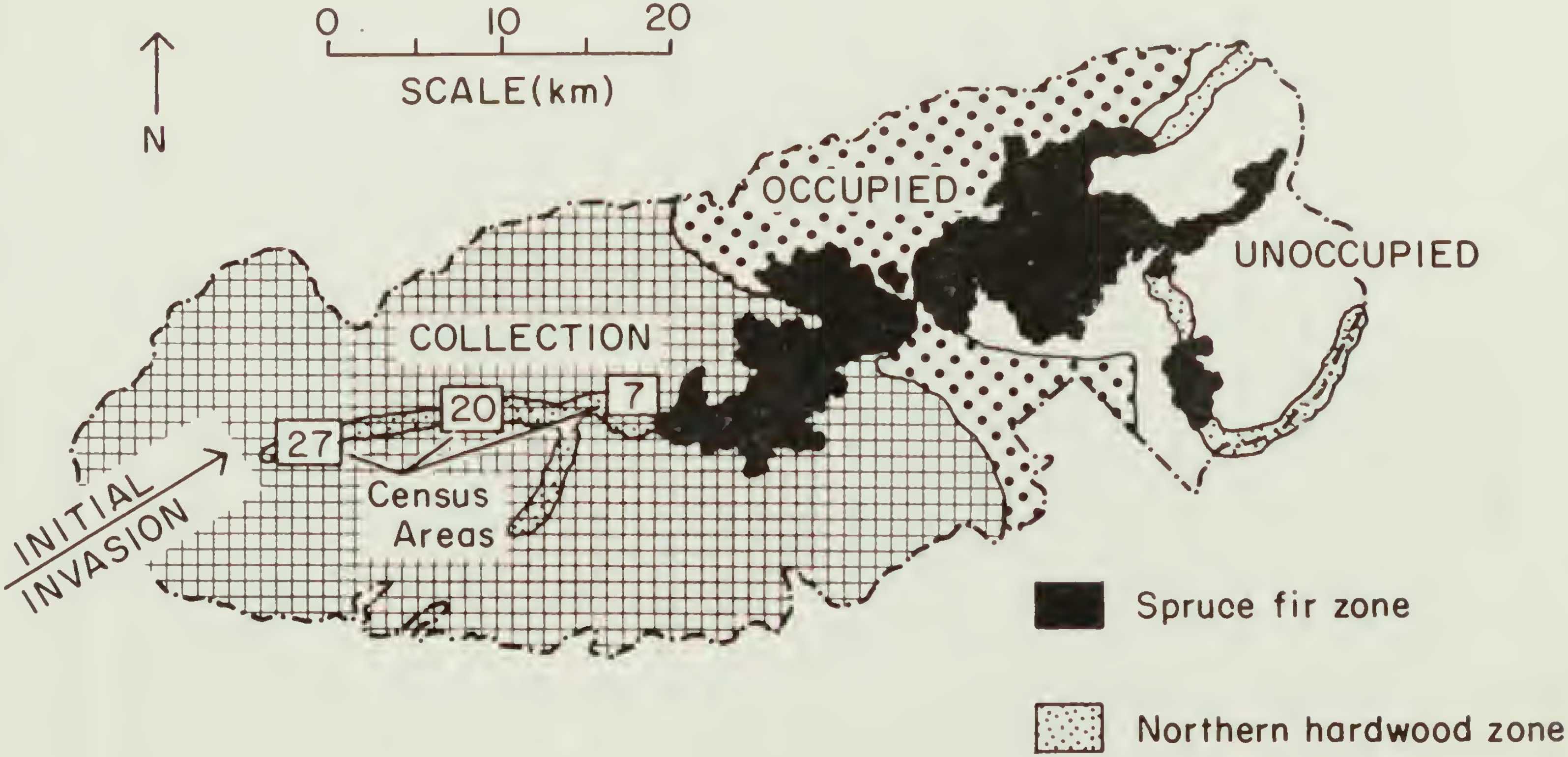

Figure 1. Map of Great Smoky Mountains National Park, showing collection area in the occupied western one-half of the park. Census areas occupied by wild boar for 7, 20, and 27 year are indicated.

23% oak (*Q.* spp.), 14% white pine (*P. strobus*, *Q.* spp.), 5% hardwoods (*Acer* spp., *Betula lutea*), 4% hemlock-hardwoods (*Tsuga canadensis*), 3% laurel slicks (*Kalmia latifolia*, *Rhododendron* spp.), and 2% old homesites now dominated by successional tulip poplar (*Liriodendron tulipifera*) (M. Harmon, in lit.). The high elevation range studied (11.6 km^2) was 41% covered by oak-maple forest (*Q. rubra*, *Acer rubrum*), 23% cove hardwoods (*Aesculus octandra, Tilia heterophylla*, *Fraxinus americana*), 15% northern hardwoods (*Fagus grandifolia*, *B. lutea*, *Aesculus octandra*), 15% hemlock (*T. canadensis*, *Halesia caroliniana*), 3% chestnut oak, and 3% others. Elevations ranged from 549 to 945 m on the winter range and from 1,425 to 1,670 m on the summer range.

METHODS

Tissue Collections from Wild Boar

Lower jaws were collected from all animals younger than 26 months or were aged in the field by tooth eruption patterns (Diong, 1973, following Matschke, 1967). This method is accurate for 2-month age groupings. Animals older than 26 months were aged to the nearest year by counting the cementum annuli in the third incisor or field-aged by molar wear patterns (Kozlo, 1973), which were later corrected by linear regression established from annuli counts. Fetuses in pregnant females were sexed, counted, and aged by crown-to-rump length (Henry, 1968). Young piglets usually remained near the trap when their mother and/or part of the litter were captured -- the number of these piglets were recorded. Sex and age compositions were tested with a four-dimensional contingency table (Fienberg, 1970) utilizing elevation (high or low), sex (male or female), age (0-1 year, 1-2 year, and adult

or 2+ year), and harvest (undisturbed or heavily harvested $>$ 1 year) as variables. The best models were selected with partitioning by goodness-of-fit tests.

Conditional Information

Blood samples were collected from shot or immobilized wild boar as soon as the animals could safely be handled. Using Vacutainer blood-collecting techniques, clotted and non-clotted (EDTA used as an anticoagulant) whole blood samples were taken for analysis. Blood was drawn from the anterior vena cava and via heart puncture. Clotted whole blood samples were centrifuged at 1,500 rpm for 10 minutes, sera removed and frozen. Whole non-coagulated blood specimens were kept refrigerated and transported daily to the University of Tennessee Memorial Hospital, Knoxville, Tennessee, for hematological analysis. A model F Coulter counter was used to determine red and white blood cell counts and packed cell volume. Hemoglobin values were obtained from a Coulter hemoglobinometer. Analysis of 21 sera biochemical parameters were provided from a Technicon SMAC System at Fort Sanders Presbyterian Hospital, Knoxville, Tennessee.

Density Information

Counts of free-ranging wild boar were made while walking trails with the aid of a flashlight from about 2030-0200 h. Only still, dry evenings were censusd to maximize detection of rooting animals. The perpendicular and radial distance to each group was measured or estimated along with the angle from the observer's path, and wild boar densities estimated by the transect technique of Eberhardt (1969), as expanded in Caughley (1977). Since the trail system was not representative, estimates were calculated for each forest type and then corrected for the availability of each forest type.

Food Availability

The availability of major forages of wild boar was estimated only in those forest types receiving the majority of feeding activity, since a detailed analysis of each forest type was beyond time or resources. Analyses were designed to distinguish major differences between food economies. Subterranean forage availability was sampled in northern hardwood stands (n = 80 soil samples, Howe et al., in press) and in low elevation, tulip poplar stands (n = 24 soil samples). Each soil sample was randomly located within a preferred stand and was 0.1 m^2 on the surface and 15 cm deep. Roots and macroinvertebrates were separated from the soil, rinsed with water, and oven-dried. Understory herb and shrub biomass was obtained from Whittaker (1966) and from an additional 10 plots of 1 m^2 clipped plots to correct for understory alteration due to the wild boar occupation. Hard mast production on the winter range was determined through numerical mast ratings on a yearly sample of 40 trees (Whitehead, 1967, modified from Sharp, 1958). Estimated for each tree were: (1) the percentage of the tree crown producing acorns, (2) the percentage of twigs in the productive crown bearing acorns, and (3) the average number of acorns per productive twig. Whitehead (1967) provided acorn production figures using tree basal area and the corresponding numerical ratings from a sample of trees in east Tennessee that were first rated, then cut down, and all the acorns collected. Basal areas at breast height for mast-producing trees on the winter range was provided by M. Harmon (in lit.) based upon sampling in 70 plots of 0.1 ha. We expressed all food availability as kg/ha on a dry weight basis.

Mortality rates were calculated from a life table of those captured and harvested wild boar which were aged by tooth eruption or annuli (Caughley, 1976; Deevey, 1947). Piglets observed near trapped sows were also included to partially compensate for underrepresentation of juveniles in capture samples (Caughley, 1976).

RESULTS AND DISCUSSION

Density and Population Trends

A total of 14 km were hiked during census in the summer of 1976 (n = 9 nights, Schaffer, 1979), 72 km in 1977 (n = 25 nights), 55 km in 1978 (n = 17 nights), and 15 km in 1979 (n = 5 nights). A total of 158 groups of wild boar were observed. Assumptions of the techniques were met since all animals flushed directly or diagonally downslope thereby minimizing the chance of counting an animal more than once, and group size did not influence flushing distance ($r = 0.28$, $P < 0.10$). Wild boar densities on the study area occupied for 20 years were low in 1976 following a poor mast year, then increased 46% and declined 4% following two successive good mast years in 1977 and 1978, respectively, and then declined 64% following a mast failure in 1979 (Fig. 2). Wild boar density in 1978 was 43% higher near the invasion front than in the areas occupied 20 and 27 year (Mann-Whitney U-test; $z = 1.6$, $P < 0.10$; Fig. 2). Population estimate for the occupied northern hardwood zone of 54 linear km, 1.5 km on either side of the ridge (the "core" park population), was 1,050 $\pm$ 320 ($\bar{X} \pm$ 95% CI) in 1978. Densities in 1976 in low elevation oak/pine/pasture habitat were less than 2.0/km^2 (Shaffer, 1979). In 1977, the known minimum number of wild boar on the 20-year occupied area was 53 individuals on 11.6 km^2 (4.6/km^2), or 42% less than the line transect estimate. This information strengthened the line transect estimate since many unmarked and unrecognizable animals were observed and the known minimum number was therefore low.

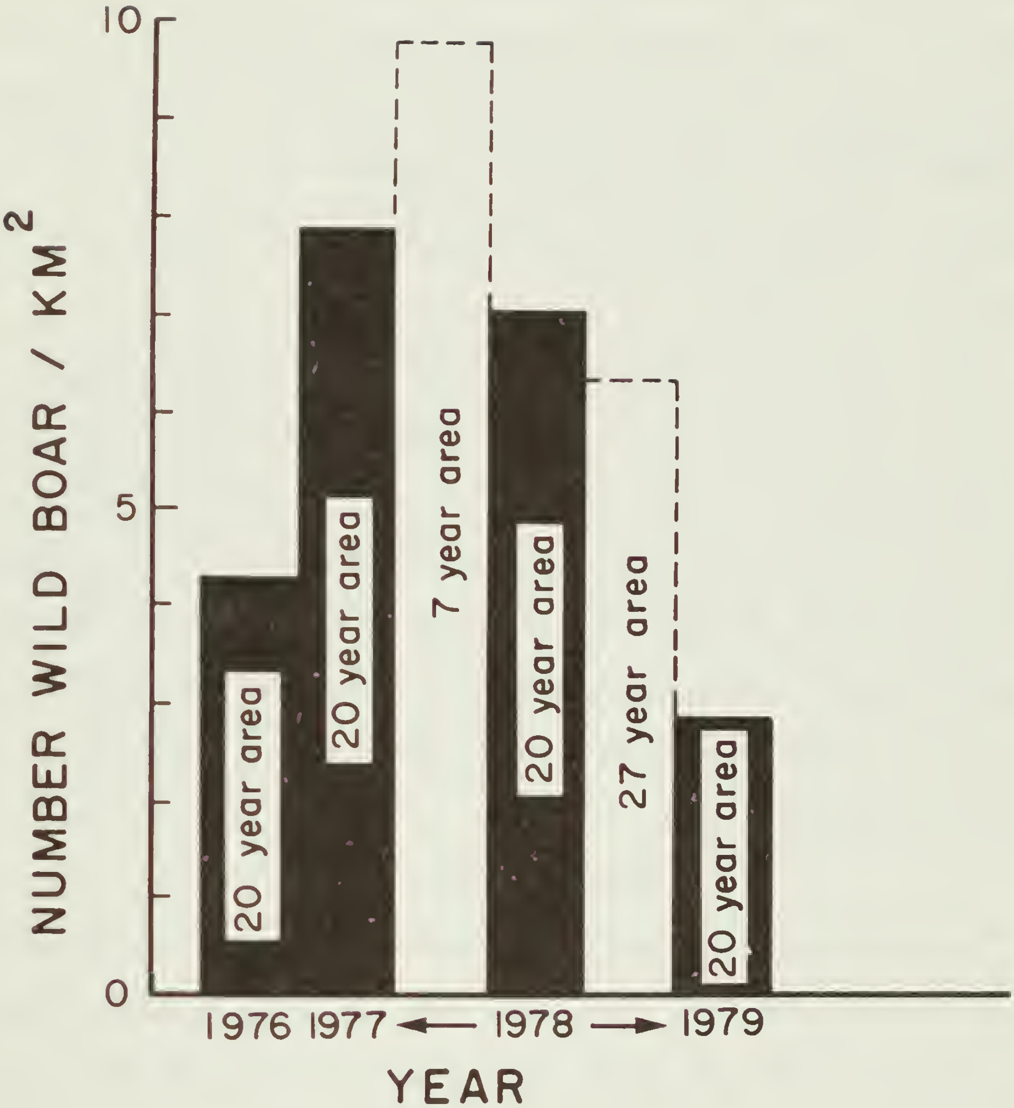

Figure 2. Population trend for wild boar in a northern hardwood forest area (11.4 km^2) occupied for 20 year; and also, in 1978, estimates for areas occupied for 7 and 27 year.

Low elevation densitites in GRSM were slightly lower than those reported from most comparable European studies (Donaurov and Teplov, 1938; Haber, 1969; Jezierski and Myrcha, 1975; Pucek et al., 1975) and nearly identical to those reported from Cherokee National Forest, Tennessee (Henry and Conley, 1972). Seasonal densities at the high elevations, however, are among the highest reported (Munzel, 1971; Heptner et al., 1966).

Peak densities of wild boar were found 7 years after initial occupation of an area, with stability suggested between 20 and 27 year of occupation. A decline or "crash" period following invasion (Riney, 1964; Caughley, 1970; Challies, 1975; Clarke, 1976) has not been observed yet in GRSM. Population fluctuations due to weather-controlled mast availability may mask or dampen abrupt oscillations, as a heavy harvest greater than one-half the rate of increase could do (Caughley, 1977).

Food Abundance

Production of hard mast varied greatly during four consecutive years (Table 1). In 1976, 1977, and 1979, which we rated as moderate or abundant mast years, the production of mast-producing stands on the winter range (86% of the range) averaged 51.0 ± 6.2, 66.2 ± 8.0, and 32.6 ± 3.9 kg/ha ($x \pm 95\%$ C.I.), respectively. Production in 1978 was only 20.7 ± 2.5, or a failure.

Northern hardwood stands in summer provided the most food/ha for wild boar (Table 2) but these stands were very small in area (1.7 km^2). Mixed oak/pine winter habitat provided less food/ha but over a much

Table 1. Dry weight production of hard mast (kg/ha) on the low elevation, winter range (31.4 km^2).

Mast Producing Trees	Mean Basal Area (m^2) Oak Type (2.3)	Yellow Pine-Oak (.49)	White Pine (.14)	Mean Production (kg/ha) in Oak-Pine Types (0.86) 1976	1977	1978	1979
Quercus rubra	0.6	1.3	0.02	12.0	7.1	0.7	0.7
Q. prinus	5.8	1.9	0.9	14.2	40.0	7.8	12.0
Q. alba	5.6	0.07	0.1	9.9	5.0	5.7	9.2
Q. velutina	1.6	0.13	0.3	1.4	9.9	1.4	0.1
Q. coccinea	1.9	0.02	1.7	7.1	2.1	5.0	0.7
Carya spp.	0.5	4.6	0.05	6.4	2.1	0.1	9.9
TOTAL	16.0	8.02	3.07	51.0	66.2	20.7	32.6

Table 2. The availability of major foods to European wild boar, their utilization, and the relation to movements and fat index values. Presented are two summers, 1977 and 1978; two winters of abundant mast, 1976-77 and 1977-78; and one of mast failure, 1978-79.

Forest Types (Proportion of Range)	SUMMERS: Northern Hardwood Forest (0.15)		WINTERS: Abundant Mast: Mixed Oak/Pines, from Table 1 (0.86)		WINTERS: Mast Failure: Mixed Oak/Pine (0.86) and Old Homesite - Tulip Forest (0.02)	
FOOD CATEGORIES:	kg/ha	Proportion of diet	kg/ha	Proportion of diet 3/	kg/ha	Proportion of diet
1. ROOTS						
Claytonia virginica	138 ± 9	(0.59) 1/				
Dioscorea batatas					74 ± 35	(0.72) 2/
Other roots	54 ± 5	(0.11)			89 ± 84	(tr)
2 HERBACEOUS VEGETATION	7	(0.28)	n.a.	(0.07) 2/	n.a.	(0.16)
3. SHRUBS, CURRENT TWIGS	1	(0.01)				
4. SOIL MACROINVERTEBRATES	8	(0.01)			12	(0.01)
5. HARD MAST						
Quercus spp.			44 ± 6.0	(0.88)	21 ± 2.8	(0.08)
Carya spp.			6 ± 0.4	(0.02)	0.1	

Table 2. Continued

	SUMMERS		WINTERS			
			Abundant Mast		Mast Failure	
Forest Types (Proportion of Range)	Northern Hardwood Forest (0.15)		Mixed Oak/Pines, from Table 1 (0.86)		Mixed Oak/Pine (0.86) and Old Homesite - Tulip Forest (0.02)	
FOOD CATEGORIES:	kg/ha	Proportion of diet	kg/ha	Proportion of diet 3/	kg/ha	Proportion of diet
6. OTHER				(0.02)		(0.03)
TOTAL PALATABLE FOOD	208	(1.00)	50	(1.00)	196	(1.00)
RELATIVIZED AVAILABILITY (proportion of area by kg/ha)	31		43		20	
MEAN SEASONAL HOME RANGE SIZE (n = 18) in ha 4/	369 ± 182		315 ± 284		1069 ± 641	
MEAN Km MOVED PER HOUR (n = 744 h) 4/	0.15 ± 0.037		0.065 ± 0.017		0.404 ± 0.144	
MEAN FAT INDEX	2.8		3.2		2.3	

1/ Dry weight proportion.

2/ Volume Proportion.

3/ Abundant mast diet values averaged from Scott and Pelton (1975) and our sample of nine stomachs.

4/ Summer Sample = 49 stomachs; Mast Failure = 20 stomachs. n.a. = Not available.

larger area (29.3 km^2 of oak/pine forest), and acorns were probably more easily obtained than subterranean foods.

The availability and dispersion of food influenced wild boar movements. When mast was abundant, wild boar greatly restricted their movements and often fed for acorns and bedded on the same warm, south-facing oak/pine slopes (Singer et al., in press). Wild boar seasonal home ranges then were the smallest, movements were the least, and the fat index the highest (Table 2). Although food was abundant in northern hardwoods, movements were much greater there; wild boar moved upwards from daybeds and wallows located 0.5 to 1.5 km down the ridgeside to feed each night in the ridgeline northern hardwoods (Singer et al., in press). The greatest movements occurred during the mast failure when food was scarce, because the old homesites (tulip poplar stands) where food was available were very limited in area (0.02%) and scattered. Densities of wild boar were 3.5 to 5 times greater in the northern hardwood zone, suggesting potentially greater competition for the available food. In a Polish preserve, densities of wild boar (10 animals/km^2) comparable to those we documented were only obtained through year-long intensive supplemental feeding (Jezierski and Myrcha, 1975); and fresh rooting there never exceeded 1,000 m^2/ha. In the northern hardwood forest type in GRSM, however, summer rooting averaged 8,000 m^2/ha (Bratton et al., in press).

Condition

The effect of age on the fat index was significant ($F = 6.30$, $P < 0.035$): the effect of breeding status in adults (1.6+ years) was significant ($F = 4.69$, $P < 0.05$); but the effect of food economy was not significant ($P > 0.95$). During mast failure on winter range,

generally abundant food from September - November tended to mask declining conditions in December - February (Fig. 3). We therefore analyzed the effect of months on the fat index during this period and found the relationship to be significant (F = 7.2, $P < 0.001$). During the mast failure, more wild boar were in poor condition; among age classes, more animals were in poor condition in the 0.6 to 1.5 year class; and among sexes, more lactating females were in poor condition.

The fat index was apparently a valid condition parameter. Fat index was rank correlated with blood assays for total protein, albumin, cholesterol, glucose, and white blood cells (Spearman rank correlation, r_s = P 0.05, (Table 3)).

During February - March of the mast failure, 11 wild boar were found dead or dying of presumed starvation: one adult male, five adult females, and four animals aged 10 to 14 months (one male, three females). Two of the adults were radio-collared individuals that we were monitoring. Few adult males died and many even remained fat throughout the food shortage. Females,particularly those accompanied by piglets aged 10 to 14 months, were stressed, suggesting that they had lactated up to August and probably entered the period of food shortage with fat reserves already depleted. High parasite loads (*Metastrongulus* spp., *Stephanurus strontatus*) accompanied the malnutrition (P. Smith, in lit.). Normal weight of age class 12-14 months (37.5 $\pm$ 6.6 kg) were reduced to only 28.7 $\pm$ 6.7 kg during the mast failure (Mann-Whitney U-test, n = 18, U = 18, $P < 0.15$); weights of adult males (78.6 $\pm$ 6.2 kg) were reduced to 70.2 $\pm$ 4.7 kg (Z = 2.11, n = 44, $P < 0.05$); and weights of adult females (66.5 $\pm$ 7.7 kg) were reduced to 61.2 $\pm$ 12.0 kg (Z = 2.53, n = 39, $P < 0.10$). Small samples in other age classes during the failure precluded analysis.

Blood samples were collected from 70 wild boar (38 male, 32

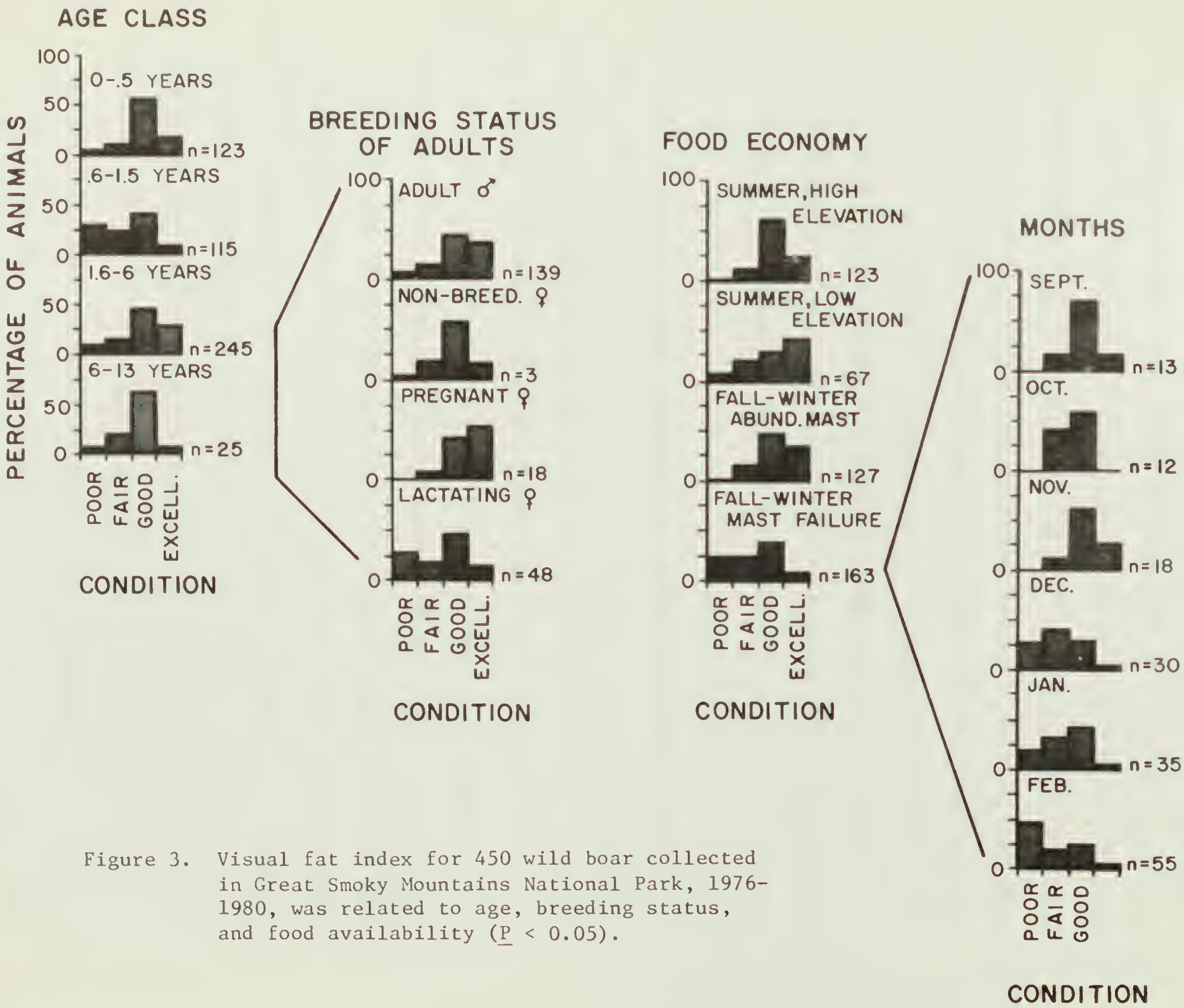

Figure 3. Visual fat index for 450 wild boar collected in Great Smoky Mountains National Park, 1976-1980, was related to age, breeding status, and food availability ($\underline{P} < 0.05$).

Table 3. Significant effects of food economy on both hematology and blood chemistry assays in wild boar.

Assay (Units)	Spearman Rank Correlation with Fat Index	FOOD ECONOMY Winter, Mast Failure = Summer, Hi Elev.		Summer Lo. Elev. = Winter, Ab. Mast
			<<	
Total protein (g/dl)	0.44*	6.9 ± 0.3		7.0 ± 0.3
Albumin (g/dl)	0.45*	3.3 ± 0.5	<<	3.7 ± 0.3*
Cholesterol (mg/dl)	0.42*	78 ± 11	<<	111 ± 12
Glucose (mg/dl)	0.47*	190 ± 44	>>	136 ± 35
Uric Acid (mg/dl)	0.13	0.5 ± 0.2	<<	1.0 ± 0.6*
Calcium (mg/dl)	0.19	9.8 ± 0.5	<<	10.9 ± 0.8*
Phosphorus (mg/cl)	-0.12	8.4 ± 0.7	>>	6.6 ± 1.7*
Electrolyte Balance ($Cl + Co_2$)	-0.13	18.2 ± 4.4	<<	25.6 ± 3.2*
Packed cell volume (% cells)	0.04	40.9 ± 4.8	<<	42.6 ± 2.7*
White blood cells counts (ten thous/mm^3)	0.25	8.7 ± 1.8	<<	13.4 ± 6.8*
Albumin/Globulin Ratio	0.42*	1.04 ± 0.20	<<	1.96 ± 1.03*

* Denotes significance at $\underline{P} < 0.05$ level

female). Twenty were first trapped and then shot, 16 were immobilized, 18 were shot in the field, and 16 were trapped and then physically restrained. Analysis of variance tests indicated no differences among sex or age classes for animals more than four months old, as Williamson and Pelton (1975, 1976) found. Animals $>$ 4 months old were pooled and samples between food economics compared using analysis of variance for unequal sample size. Sample sizes were as follows: mast failure - 17 animals; abundant mast = 21 animals; summers, high elevations = 9 animals; summers, low elevations = 23 animals. Twelve assays were not different between food economies. Seven assays (Table 3) were significantly higher during winters of abundant mast, and summers, low elevations than other periods ($P < 0.05$) (albumin, cholesterol, uric acid, calcium, electrolyte balance, packed cell volume, white blood cells, and albumin/globulin ratio) while 13 assays were not different (Table 4).

Lack of correlations in other assays may have been due to the use of different restraining techniques and pooling monthly samples within seasons. Glucose, packed cell volume, red blood cell count, and hemoglobin parameters are sensitive to handling techniques and excitability of the animal (Franzmann, 1972; Drevemo et al., 1974; Franzmann and LeResche, 1978; Karns and Crichton, 1978; Wesson et al., 1979). Total protein correlates with condition but is a relatively insensitive test in many ungulates (Seal et al., 1972, Franzmann, 1972; Malpas, 1977). Blood urea nitrogen (BUN) generally correlates well with condition; because it is less influenced by excitability or method of handling in ungulates, it is often recommended as a condition indicator (Seal et al., 1972; Franzmann, 1972; Franzmann and LeResche, 1978). BUN values were lowest in winters with abundant mast (8 mg/dl, $P < 0.05$) but were not different among the other three food economies (14 mg/dl, $P > 0.95$). High BUN values indicate

Table 4. Results of assays not affected by food economy.

Assay (units)	$\overline{X}$ ± 95% C.I.
Serum iron (mcg/dl)	145 ± 19
Triglyceride (mg/dl)	47 ± 12
Total Bilirubin (mg/dl)	0.06 ± 0.05
Alkaline Phosphatase (U/L)	78 ± 21
SGOT[a] (U/L)	85 ± 32
Globulin (g/dl)	3.5 ± 0.5
Creatine (mg/dl)	1.4 ± 0.1
Sodium (m Eq/L)	142 ± 4
Chloride (m Eq/L)	96 ± 2
Blood Urea Nitrogen (mg/dl)	11 ± 3
Hemoglobin (gm/100 ml)	14.0 ± 7.1
Red blood cells (millions/mm^3)	6.8 ± 0.4
BUN/Creatine ratio	9.3 ± 4.4

[a] Serum glutamic oxalacetic transaminase.

a high protein meal within the last 4-8 hr, and remaining in traps for part of the night might have reduced these values in wild boar, thereby obscuring patterns. The two abnormally high BUN values, 48 and 44, were in a 20 month-old female and an 8 month-old male, respectively, both of which were field-shot during the summer while on herbaceous diets. Acorns are low in protein and high in fat (Short and Epps, 1976), suggesting that a recent meal of acorns would not elevate BUN values.

Sex and Age Composition

Information was gathered on 550 wild boar; 405 of these were dissected and 145 were restrained and released alive. Fifty-four wild boar were released to the park for research purposes; 91 were transported for release on State game lands outside the Park. Males predominated in the sample of wild boar in ratio of 1.18:1.00 (n = 550, 298 male: 262 female). However, considerable sex and age variations occurred between different food economies and units with different harvesting histories. At the onset of our collections, 25% of the animals taken in previously undisturbed northern hardwoods habitat were adult females (n = 97), but 1 year after harvesting began, only 14% were adult females (n = 42, Fig. 4). Only 16% of undisturbed, low-elevation summer collections were adult females (n = 71), and 0% after 1 year of harvesting (n = 13). Contingency table analysis (Fienberg, 1970) indicated that the effects of elevation on age, elevation on sex, and harvesting on sex were significant ($P < 0.05$). Collection bias toward adult females in the high elevation zone was attributed to a predominance of female/young groups in the northern hardwood forest type (Singer et al., in press), where the collections were focused. DeVos and Sassani (1977) found more adult female wild boar in mountainous habitat, and female/young groups occupied optimal habitat in other ungulate species (Cowan, 1950; Murie, 1951;

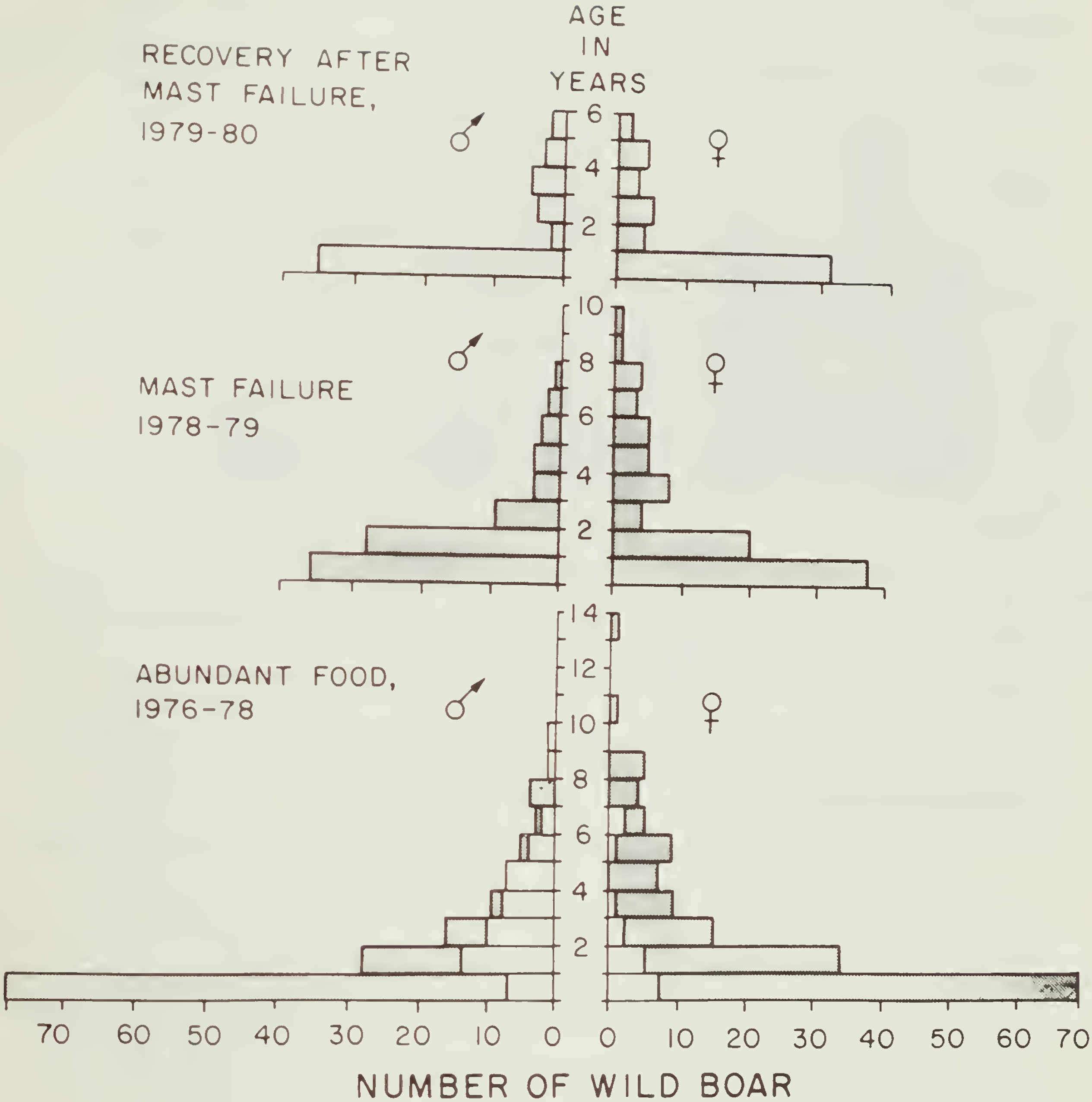

Figure 4. Age structure of 550 European wild boar collected in Great Smoky Mountains National Park during two years of abundant food, September 1976 - August 1978; one year following a mast failure, September 1978-79; and the first 7 months of recovery, September 1979 - March 1980. Animals taken in units harvested > 1 year during the period when food was constant are superimposed (white) over the unharvested sample.

Peek and Lovaas, 1968; Geist and Petocz, 1977). The predominance of adult and yearling males in the harvested units (Fig. 4) is attributed to a greater tendency of males to disperse into the vacant habitats (Singer et al., in press), a pattern also observed when other large mammals are intensively harvested (Douglas, 1971; Brooks, 1975; Smuts, 1978).

Small young are often under-represented in both shot and trap samples of ungulates (Caughley, 1977). We recorded the number of piglets near a shot or trapped sow and included them in Figure 4 partially correcting for this bias. Very young piglets are still under-represented since they are not brought forth from the farrowing nests until they are about 6 weeks old (Sludskii, 1956; Jezierski, 1977).

Births were near continuous when food was abundant (Fig. 5) and age composition varied little during the year, unlike western Europe, where a distinct April birth period occurs (Oloff, 1950; Heptner et al., 1966; Sludskii 1956; Jezierski and Myrcha, 1975). The proportion of the population less than 6 months of age varied from 30% when food was abundant to only 17% during the mast failure and to 61% when breeding recovered following the mast failure (Fig. 4).

The monthly capture sample varied greatly (Fig. 5), although effort was relatively consistent throughout the study. Wild boar were most difficult to collect when natural food was most abundant and also when densities were lowest. Number of trap nights per capture was ordered: 11 on high-elevation summer range $\ll$ 16 on winter range during mast failure $\ll$ 58 on winter range during abundant mast (Jonckheere's ordered alternative test, $\underline{S} = 36$, $\underline{P} < 0.05$; n = 6, 166 trap nights during 10 trap sessions).

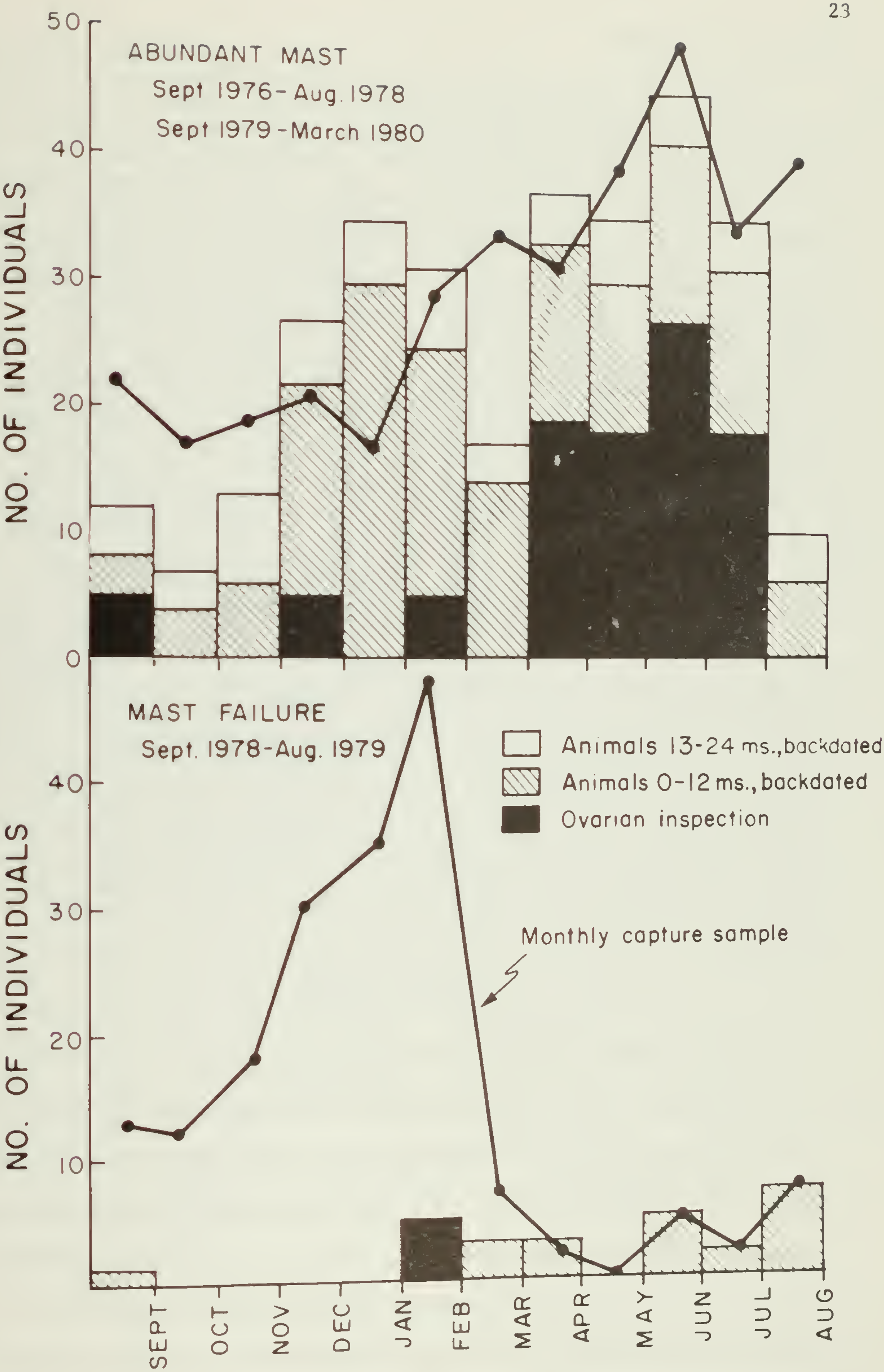

Figure 5. Monthly births of European wild boar as estimated by ovarian inspection, backdating juveniles aged 0 - 12 months and 13 - 24 months to their date of birth.

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A total of 120 cohesive groups of 423 wild boar were observed in the field or harvested, where sex and age composition could be accurately determined ($\overline{X} = 3.53 \pm 1.30$, range 1 - 24). Adult males were typically solitary (n = 21 groups) or with estrous sows (n = 4) or yearling males (n = 3). The most frequent groups were families of a female with her piglets and/or yearling (n = 36), two or more females with their young (n = 4), and piglets with no female (n = 9). These small groupings resemble those described for feral pigs (Challies, 1975; Baber, 1978) and not the large "sounder" aggregations of many females with their same-aged young that are so typical in wild boar in Eurasia (Donaurov and Teplov, 1938; Sludskii, 1956; Eisenberg and Lockhardt, 1972).

Larger groups of wild boar are more adaptive in snow for trailing and mutual rooting, in cold weather for group bedding, and when large predators are present (Sludskii, 1956). However, in equatorial climates estrous synchrony is suspected of promoting sounder groups (Eisenberg and Lockhardt, 1972). We suspect that the grouping tendency may be one of several social traits lost by this population during domestic inter-breeding.

Reproduction

Fetal litter size average 4.79 ± 0.60 (range 3 - 8, n = 24 pregnant sows), very similar to the 4.9 reported from the Cherokee National Forest, Tennessee (Henry, 1966). Litter sizes of free-ranging piglets $<$ 4 months old was 2.93 ± 0.20 (n = 57 litters) when food was abundant, suggesting 36% natal and post-partum losses. This loss is minimal, since some loss of total litters must have occurred. Litters observed in the field (n = 13) and litters in and around traps (n = 44) were pooled since sizes from both were identical. Increased fetal

litter size or greater piglet survival was indicated during September 1979 - March 1980 when the population was recovering rapidly. Litter size for $<$ 4-month-old piglets during the recovery was 3.79 $\pm$ 0.33, (Mann- Whitney U-test, $\underline{Z}$ = 2.2, $\underline{P} < 0.05$, n = 71 litters).

Henry (1966) reported the mean age of puberty in female wild boar to be 7 months, and Sweeney et al. (1979) reported mean puberty as 10 months for feral pigs. We found the age of first conception of successful litters in eight radio-collared or marked wild boar to be 16.8 $\pm$ 0.8 months (range 7.5 - 24), suggesting that younger females exhibited pseudo-estrous (Duncan and Lodge, 1960) or were inhibited from breeding through interactions with older females in family groups (Skryja, 1978). Henry's (1966) sample was based on pen-reared animals, and the increased availability of artificial food may have accelerated puberty. Female wild boar in Eurasia first successfully conceive when 18 to 20 months old, although they may conceive at 6 to 8 months when food is very abundant (Oloff, 1951; Sludskii, 1956; Briedermann, 1971).

During 2 year of abundant food conditions, 15% of young females (6 to 17 months) were either pregnant or lactating, 53% of females aged 18 months to 6 year were breeding, but only 17% of old females aged 7+ years. Litter size of young breeding females ($\bar{x}$ = 4.2) was smaller than those of prime-aged females (n = 134 sows, x^2 = 30.22, d.f. = 2, $\underline{P} < 0.001$). Other authors have reported lesser fertility and litter size in very young and old female wild boar (Sludskii, 1956; Briederman, 1971; Stube and Stubbe, 1977).

Production of two surviving litters in 1 year occurred in 3% of the females (Fig. 6). We documented double-breeding in one radio-collared female and found her nests and piglets. Another female was pregnant

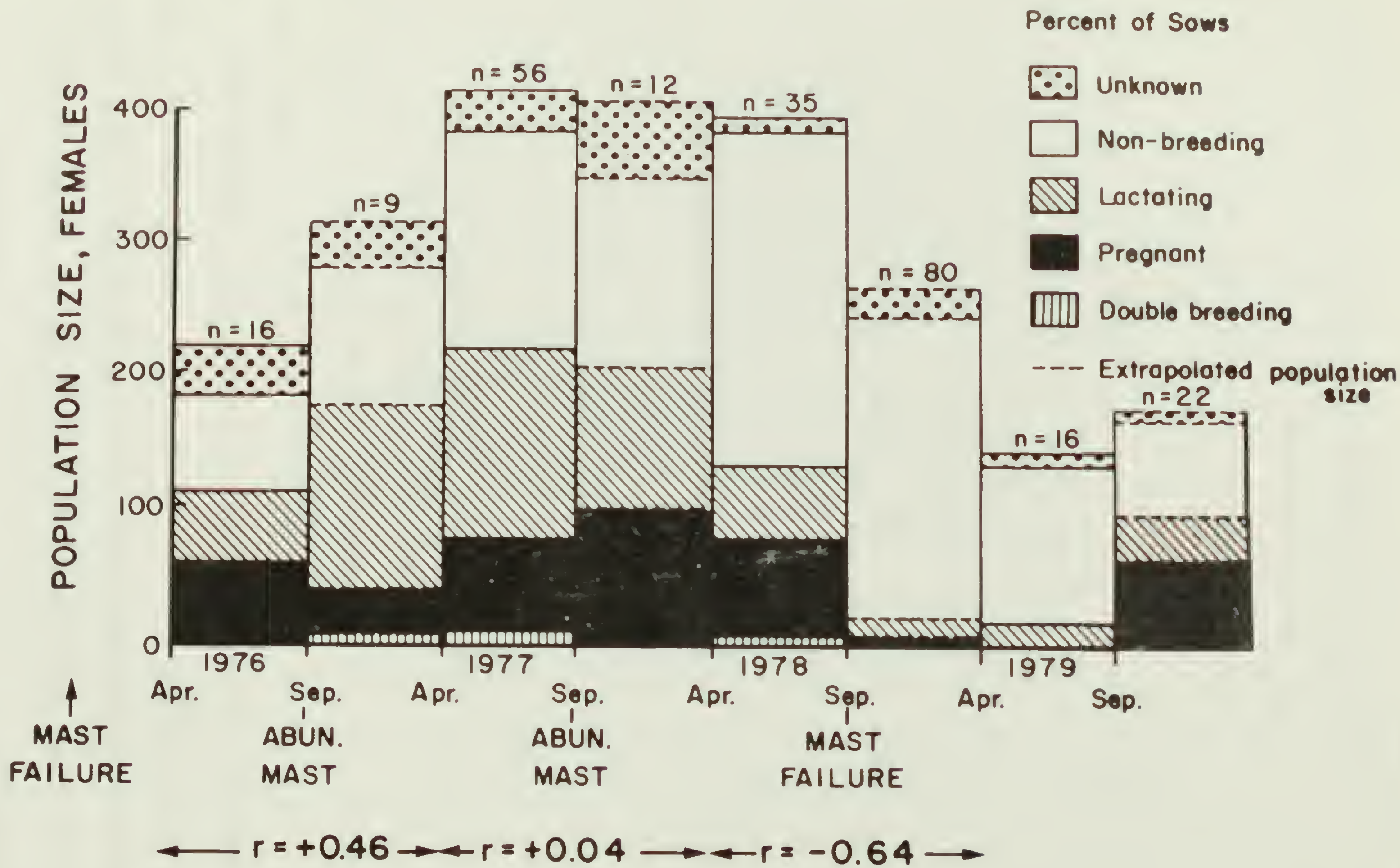

Figure 6. Breeding status of 224 female wild boar > 6 months old captured in the mast economy or September - March periods, and the root/herb economy or April - August periods, 1976-79. Female segment of the minimum core population was extrapolated from annual sex ratios observed at the high elevations. Values of r shown are observed population changes.

while suckling piglets, and the remaining four females were pregnant while accompanied by non-suckling piglets less than 6 months of age. Average interval between double litters, based on ovarian inspection and backdating the piglets at heel, was 7.1 $\pm$ 0.8 months (range 3 - 10). Double production of surviving litters is not reported in wild boar from harsh ranges in the Soviet Union (Sludskii, 1956) nor the Cherokee National Forest (Henry, 1966), but occurs regularly in Germany when food is abundant and may occur in up to 40% of the females when supplemental feeding is provided (Oloff, 1951). Henry (1966), on the other hand, found no evidence of double breeding in the Cherokee National Forest.

An average of 52% of females $>$ 6 months old bred during each season of abundant food (range 37%-56% per season, Fig. 6). When food was abundant, winter breeding rate (54%) did not differ significantly from the summer (47%) rate (n = 134, χ^2 = 0.45, d.f. = 2, $\underline{P} > 0.50$) nor did fetal litter size differ (n = 24, χ^2 = 0.73). In the 12 months following the mast failure, only 8% of the females bred (n = 246, χ^2 = 41.06, d.f. = 1, $\underline{P} < 0.001$). During each 12-month period from mast drop in September until August of the next year, 60 litters were produced per 100 females in 1978-79. The great variation in reproduction due to the mast crop is similar to that reported by Matschke (1967), but much greater than a reported 15% decreased pregnancy rate associated with mast failures in western Europe (Donaurov and Teplov, 1938). The reduction in production during a mast failure is associated with greatly decreased cycling in females rather than neonatal or prenatal losses (Matschke, 1967), although limited fetus resorption has been observed in feral pigs (Springer, 1976; Wood and Brenneman. 1978; Sweeney et al., 1979).

Henry (1966) reported higher fecundity but lower piglet survival in a winter farrowing peak (January - February) than a spring/summer farrowing peak (May - June). As a result, Henry (1966) found more juveniles in the fall population. We observed no distinct farrowing peaks, although general cessation in births from August to November (Henry, 1966; Springer, 1978; Sweeney et al., 1979) was observed (Fig. 5). Because piglet mortality is high in wild boar, if sample size is unequal between seasons, a bias in observed birthdates may occur (Fig. 5). Since Henry's (1966) sample was largely from annual fall hunting seasons and because he did not correct for unequal sample sizes, his conclusions on seasonality are questionable.

Population change was negligible from the first year of abundant mast production to the second successive abundant year (r = -07). Breeding rate in females decreased from 73% to 59% (n = 113, d.f. = 1, χ^2 = 1.97, significant at only $P < 0.17$). This decline in breeding rate occurred despite the fact that estimated mast production was 30% greater during the second abundant year (Table 2). More piglets and yearlings were present in the population during the second year of abundant food, and their suckling or presence may have inhibited estrous or receptiveness of females (Erickson and Nellor, 1964). Martinka (1974) observed low productivity in grizzly bears (Ursus arctos) in years when a high proportion of yearlings accompanied females. A high breedings rate (55%) occurred again in September 1979 - March 1980 population recovery period.

Mortality Rates

First year mortality average 61% for females and 54% for males, thereafter from age 2 years on the rate was 24% for females and 30% for males. Jezierski (1977) also found lower mortality after age 2, but

Table 5. Mortality rates for European wild boar.

European Wild Boar	Sex	Annual Mortality > 2 years	Initial Life Expectancy	Maximum Age	Ecological Longevity
Great Smoky Mountains	F	0.24	1.58	13	13+
	M	0.30	1.71	9	9+
Poland	F	0.43 (both)	1.42 (both)	9.3	7 (both)
	M				
Cherokee National Forest	M	0.51 (both)	1.52	7.6	7+
	F		1.39	8.8	5

Henry and Conley (1979) reported a constant mortality rate of 51% for each age class. Females lived longer than males (Jezierski, 1977; Henry and Conley, 1979), and life expectancy was greater than for Cherokee National Forest (Table 5). We attribute this greater survival in Great Smoky Mountains to the fact that 78% of all animals were collected from pristine, previously unharvested areas, whereas in Cherokee National Forest, hunter harvest of the population averages about 30% per year and survival is likely lower.

Only a few animals exhibited signs of senility. Jaw necrosis was observed in two males aged 6 and 9, and four females aged 9 - 13. Two of these animals were in poor condition with no visible fat reserves, although their blood assays were only moderate. One old animal, a 7-year-old male, exhibited abnormally low blood values (the lowest packed cell volume - 29.0; the lowest BUN/creatine ratio - 3.8; total protein only 5.8, and cholesterol only 54), but its collection during the mast failure (February) may also have contributed to poor condition. Eight of the nine females collected which were 7 years and older were taken from the northern hardwood zone, further demonstrating the old-age structure of those high-elevation populations when collections first began.

Male ungulates typically have higher mortality rates than females because of their greater dispersal tendencies as juveniles, and the stresses of fighting with other males during the breeding season (Cowan, 1950; Banfield, 1954; Robinette et al., 1957; Flook, 1970). Sludskii (1956) observed that male wild boar may lose 20% of their body weight during the rut in the Soviet Union, and more males die because of rut-associated fights. Although a distinct rut did not occur in GRSM, the same mortality pattern was suspected, since serious fighting wounds were

observed on adult males and the more aggressive and sexually motivated males moved more per hour than females (Singer et al., in press) and must have expended more energy in doing so. Females, on the other hand, were subjected to greater mortality during the mast failure because any female lactating during July or August entered the mast failure with depleted fat reserves and because adult females did not emigrate during the food failure. Because females were less likely to leave their home ranges and disperse, they were less likely to find those few sites where food was still available. The presence of large piglets at heel may have further reduced a sow's chances of survival through competition with her for what little food was located. The female age structure (Fig. 3) further suggested irregular mortality after the stressful breeding age (24 months) was reached.

ACKNOWLEDGEMENTS

S. Coleman and M. Myers coordinated the collection of many specimens and, among others, F. Branam, D. Hurley, M. Harmon, W. Cook, K. DeLozier, and G. Stilts assisted in the field and the laboratory. S. Bratton, R. Herrmann, and B. Evison provided invaluable study direction. G. Wood, D. Oh, P. Smith, and A. Tipton provided advice, J. Wood, M. Harmon, W. Cook, and B. Blakely reviewed the manuscript, and S. McGill typed several versions of the manuscript.

SUMMARY

1. A reproductive study of exotic European wild boar was made in Great Smoky Mountains National Park during 42 consecutive months, 1976-80. A total of 550 wild boar were either necropsied or inspected and released alive on State lands outside the park. Blood samples were taken from 70 animals. Acorn production was estimated during 4 Septembers, and subterranean foods were sampled by sorting soil samples.

2. Wild boar numbers were low in 1976 following a poor mast year, then increased 46% and declined 4% following two successive good mast years in 1977 and 1978 respectively, and then declined 64% following the severe mast failure of 1979.

3. Wild boar densities at low elevations in the park, less than $2.0/km^2$, were similar to those reported for nearby State lands and many locales in Europe. However, high elevation densities, $7.0-9.0/km^2$, were among the highest reported in the world. At peak densities in 1979, the western occupied ridgeline of GRSM (Appalachian Trail area) was accurately estimated to support 1,050 $\pm$ 320 animals, while the present park population is roughly suspected to include an additional 45% of that number, and after occupation of the entire park another 150%. Parkwide, after eventual occupation of the Cataloochee subdistrict, pig numbers should exceed 2,600 following abundant mast years, but could number as few as 1,400 following a very severe mast shortage, or a series of mast failure years.

4. Acorn production varied between 21 and 51 kg/ha, and greatly influenced wild boar movements, condition and reproduction. Litters per 100 females numbered 59, 60, and 73 following a moderate to abundant

mast production, and only 13 following a mast failure. Mean movements increased from 0.07 km/hour to 0.40 km/hour during the mast failure, and home range size from 315 ha to 1,069 ha. As a result of this greater activity and searching for less food, mean fat index dropped from 3.2 to 2.3.

5. Fat index was found to be correlated with blood assays for protein, albumin, cholesterol, glucose and white blood cells. In general, we found more lean animals in the yearling class, more lean lactating females than other sex classes, and more lean animals during the mast failure. Blood hematology and chemistry assays indicated that wild boar were in equally good condition during winters with abundant mast and summers at low elevations. The most food/ha occurred at the high elevations, and our explanation for lower condition there was the very high density and subsequent possible keen competition for the available food. Fat index declined each month from September-March following the mast failure of 1979, and in the latter part of the period, 11 wild boar were found dead or dying of presumed starvation.

6. Males predominated in our sample (298 M: 262F); however, we found that habitat and harvest history greatly influenced sex and age ratios. In the summer, we initially found more adult females at the high elevations than low elevations, 25% versus 16%. We attribute this difference to a higher food abundance along the main ridgeline, and a separation of the sexes, allowing more females to occupy the prime habitat. Our radiotelemetry studies also revealed that adult sows were living closer to the northern hardwood forest type. After one year of harvesting in any unit, the ratio of adult females dropped from 25 to 14% at high elevations, and from 16 to 0% at low elevations. These changing ratios demonstrate the greater

mobility of males and a greater likelihood for them to enter habitats vacated by intensive harvesting of the resident animals.

7. Trap success was directly proportional to movements of wild boar and inversely to food availability. Numbers of trap nights per capture was 11 on high elevation-summer range, $\ll 16$ on winter range-mast failure, and $\ll 58$ on winter range-abundant mast. Even under the very best of conditions, wild boar were difficult to trap.

8. Average group size was 3.53 ± 1.30, and most groups were sows with young and/or yearlings. The large "sounders" or groups of several sows with their even-aged young, which are so typical of European and Asian ranges, were absent.

9. Fetal litter size average 4.79 ± 0.60. Litter size of free-ranging piglets <4 months old was 2.93 ± 0.20. Both of these values increased slightly during September 1979 - March 1980, a population recovery period.

10. About 3% of adult females produced two surviving litters in one year. Average interval between litters was 7.1 ± 0.8 months. Double production occurs at even higher rates in wild boar in Europe, but apparently does not occur in the northern Soviet Union and on State lands adjacent to GRSM.

11. In winter an average of 54% of adult females were breeding, either lactating or pregnant, and 47% during summer. We found no distinct farrowing peaks, although there were fewer births in the August-November period.

12. We estimated first year mortality for females of 61% and for males, 54%; but after 2 years of age, the rates dropped to 24% and 30%, respectively. These rates are very similar to a park in Poland. However, the Great Smoky Mountains animals lived longer than those from Cherokee National Forest. This is understandable since the State herd is harvested at 30+% per year, while about 78% of our sample from Great Smoky Mountains came from pristine, previously undisturbed areas.

MANAGEMENT IMPLICATIONS

1. Wild boar demonstrated an ability to rapidly reoccupy habitats vacated by intensive harvesting, such as the Gregory Bald and Cades Cove areas. Therefore, harvest quotas are not useful for units smaller than the entire park. At peak densities following abundant mast crops, our estimates suggest that roughly 800 animals would need to be taken to reduce the population, and about 1,400 to effectively reduce rooting pressure. After eventual occupation of the entire park, these approximate quotas would increase to 1,400 and 2,400. respectively. After a mast failure, these quotas could potentially decrease by as much as 60%.

2. We documented a tendency on the part of adult males, yearling males and possibly some young sows to disperse from their established home ranges during a mast failure. The implication is that these classes will be the most likely to invade new unoccupied habitat, such as the Cataloochee quarter or new range NE of the Park, during mast shortages. This potential will exist every 3-5 years. Supporting this hypothesis, a handful of animals invaded Cataloochee during 1975 and 1979-80, and the Cosby area in 1973 -- all mast failure years. We were, however, unable to document the sex or age of these dispersers.

3. The wild boar population in GRSM recovered rapidly following 2 mast shortage periods. The recovery of about 40% population size occurred in a 12 month period in 1977, and one of 60% was apparently about 1/2 replaced in a 12 month period when the study terminated. Our interpretation is that, when food is abundant, this population could recover from rather severe 40-60% drops in only a 12-24 month period. Recovery from a heavy harvest should be similiar to that observed for food failures. Recovery periods were characterized by breeding in 59-73% of sows > 6 months of age, and by double breeding in about 4% of adult sows.

4. Collections by shooting and trapping were labor and cost intensive. Efforts for this research study alone involved the movement and transportation of a 2-3 man crew to the high-elevation backcountry, maintenance of 3-4 pack horses, and horse-packing of > 60 tons of bait, supplies, equipment, traps and enclosures into backcountry sites over the 4-year period. Because of the costs, control of this population with conventional trapping and shooting techniques is not recommended. At times, as many as 58 trap nights were required to trap a single animal.

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APPENDIX

Table 6. Estimated wild boar in Great Smoky Mountains after stratification of occupied and potential habitat, 1978.

Ridgeline Area	LINEAR KILOMETERS OF HABITAT				Estimated Wild Boar	Total Kilometers Censused
	High 1/ Density	Medium Density	Low Density	Zero Density		
Occupied:						
1. Appalachian Trail-East	13.7	20.5	4.8	15.2	1050 ± 320	54.2
2. Welch Ridge	6.0	4.0			205 ± 62	
Unoccupied:						
1. Appalachian Trail-West	4.6	1.0	9.2	34.3		51.1
2. Balsam Mountain		0.0	12.1	15.4		27.5
3. Cataloochee Divide		12.8	2.4	0		15.2
4. Mount Sterling		5	1.6	7.5		9.6
Unoccupied TOTAL	4.6	14.3	25.3	59.2	498 - 599	103.4
GRAND TOTAL	24.3	53.1	30.1	74.4	1349 - 1854	171.9

1/ Estimated densities of wild boar: high = 19+; medium = 11-19; low = 8-10 wild boar/linear km of ridgeline.

Table 7. Estimated wild boar numbers and corresponding harvest quotas.

Migratory "Core" Population 1/	Population Size (1.00)	Annual Population Recruitment (0.0 - 0.44)	Annual Quota to 3/ Reduce Population (0.05 - 0.46)	Annual 4/ Quota to Reduce Impacts (0.90)	Current Harvest Level
1. At peak density, after two consecutive years of abundant Mast.	1050 ± 320	460	550	900	163 (.15)
2. Low density after a mast failure.	672 ± 205	0	> 34	462	163 (.24)
3. Peak density, after occupation of the Cataloochee Divide	1600 ± 488	736	880	1440	
Western half of park, migratory and non-migratory populations. 2/	1527	702	840	1373	163 (.11)
Parkwide, after occupation of entire Catatoochee subdistrict.	2627	1208	1445	2368	

1/ Based upon stratification by habitat quality of unoccupied and occupied high elevation range, and line transect census (n = 56 nights, 156 km).

2/ Nonmigratory population estimated to be 0.83 of migratory population.

3/ Varies depending upon mast production that year.

4/ Based upon severe damage observed, even after intense harvest (0.55) and wild boar decline after mast failure (0.64), and findings of New Zealand foresters with other exotic ungulates we arrived at a 0.90 quota to reduce all impacts.

Figure 8. Stratification of wild boar densities 1.5 km on either side of central and peripheral ridges of Great Smoky Mountains National Park into 0, low = 8-10 animals/km^2, medium = 11-19/km^2, and high = 19+/km^2 categories. Also, included are predicted densities for ridges as yet unoccupied, Balsam Mt., Cataloochee, and Mt. Sterling, based upon the amounts of gray beech, northern hardwood and mixed oak forests present.

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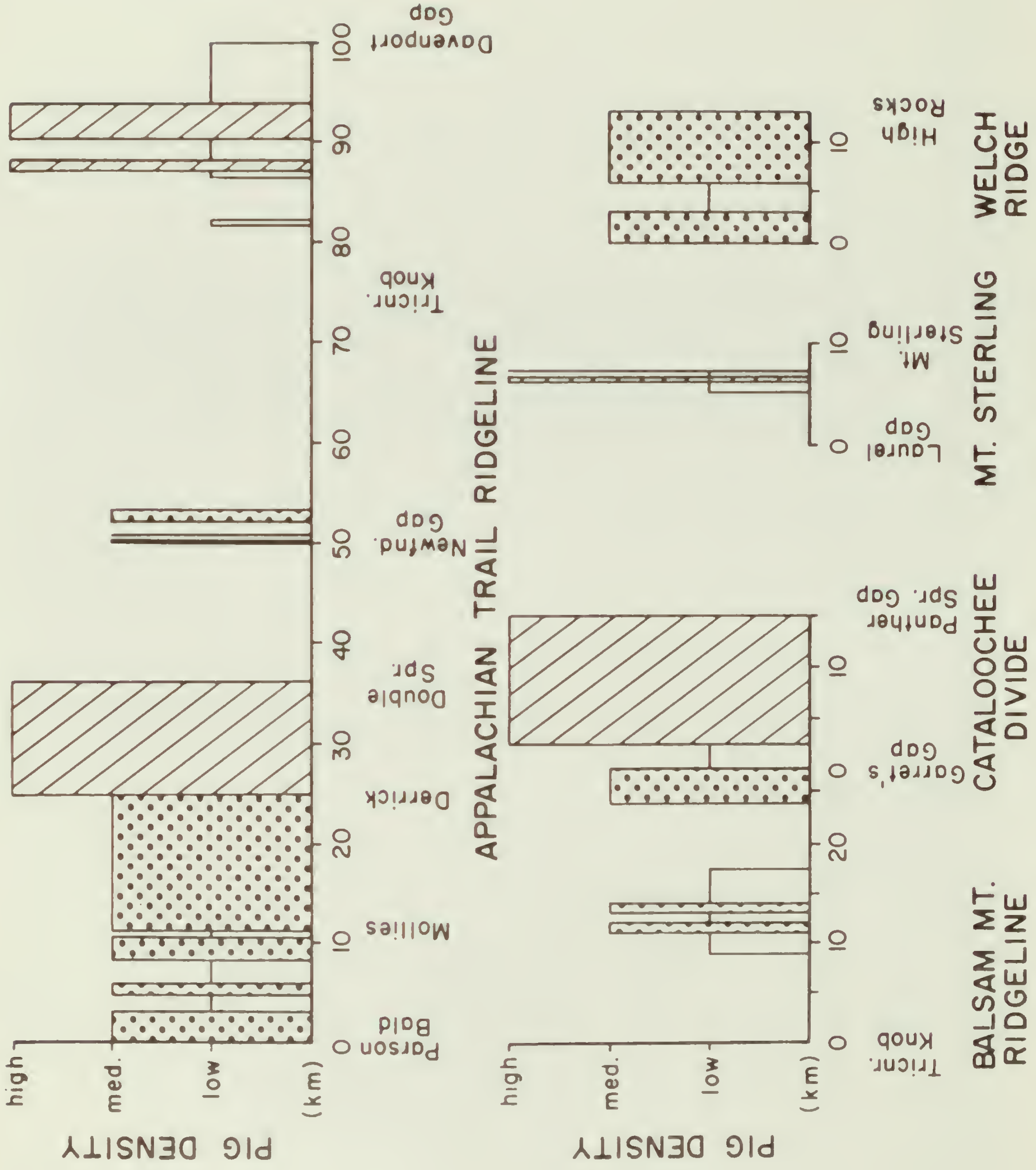
PIG DENSITY
high
med.
low
(km)
Parson Bald
Mollies
Derrick
Double Spr.
Newfnd. Gap
Tricnr. Knob
Davenport Gap
APPALACHIAN TRAIL RIDGELINE
Tricnr. Knob
BALSAM MT. RIDGELINE
Garret's Gap
Panther Spr. Gap
CATALOOCHEE DIVIDE
Laurel Gap
Mt. Sterling
MT. STERLING
High Rocks
WELCH RIDGE

Figure 9. A graphical presentation of the closer similarity of grouping tendency in the mixed wild boar of Great Smoky Mountains to feral pigs. Sources were data from this study, feral pigs - Baber (1978), Singer and Stoneburner (unpubl. data), and wild boar native ranges Sludskii (1956), Eisenberg and Lockhardt (1972).

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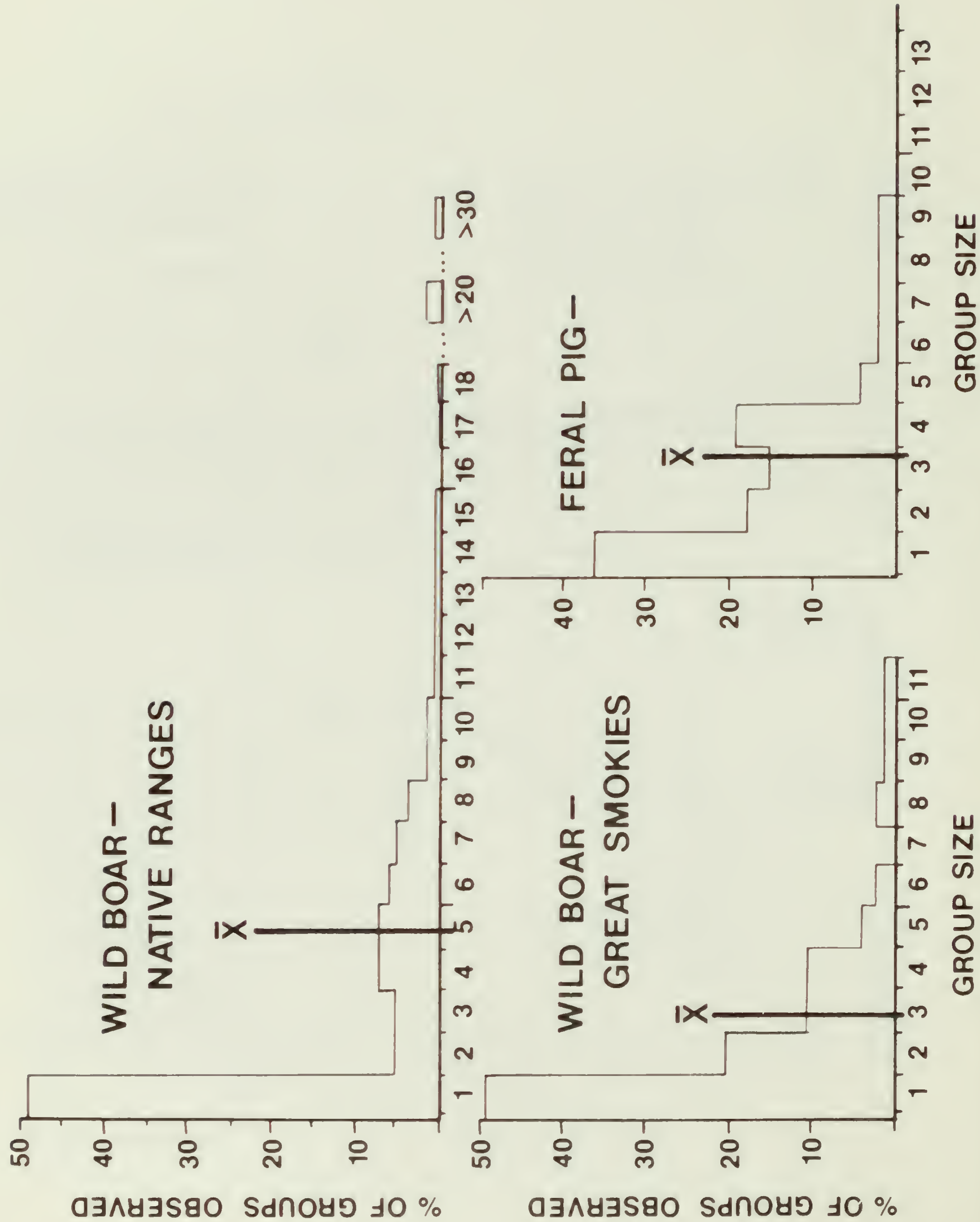
WILD BOAR – NATIVE RANGES
WILD BOAR – GREAT SMOKIES
FERAL PIG –
% OF GROUPS OBSERVED
GROUP SIZE
X̄
>20
>30

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the wisest use of our land and water resources, protecting our fish and wildlife, preserving the environment and cultural value of our national parks and historical places, and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to assure that their development is in the best interests of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.